TAXONOMY OF NORTH AMERICAN SPECIES OF *ZIZANIA* (POACEAE)

EDWARD E. TERRELL

Department of Plant Biology
University of Maryland
College Park, MD 20742-5815, U.S.A.

PAUL M. PETERSON

Department of Botany
National Museum of Natural History
Smithsonian Institution
Washington, DC 20560, U.S.A.

JAMES L. REVEAL

Department of Plant Biology
University of Maryland
College Park, MD 20742-5815, U.S.A.

MELVIN R. DUVALL

Department of Biology and Microbiology
South Dakota State University
Brookings, SD 57007-0595, U.S.A.

ABSTRACT

The grass genus *Zizania* (Poaceae: Oryzeae) is defined to include four species, three of temperate North America and one of eastern Asia. Keys, descriptions, distributions, and synonymies are provided for the North American entities: *Z. aquatica*, *Z. palustris* and *Z. texana*. We discuss recent literature and the possible origin of *Z. palustris* var. *interior*.

RESUMEN

El género de gramíneas *Zizania* (Poaceae: Oryzeae) se define como un género con cuatro especies: tres de la parte templada de Norteamérica y una de Asia oriental. Se incluyen claves, descripciones, distribuciones y sinonomias para las entidades norteamericanas: *Z. aquatica*, *Z. palustris* y *Z. texana*. Examinamos la bibliografía reciente y el origen posible de *Z. palustris* var. *interior*.

The genus *Zizania* (Poaceae: Oryzeae: Zizaniinae) is defined here to include four species. Three are North American (*Z. aquatica* L., *Z. palustris* L., and *Z. texana* Hitchc.) and a fourth (*Z. latifolia* (Griseb.) Turcz. ex Stapf) is native to eastern Asia. *Zizania aquatica* and *Z. palustris* are important constituents of aquatic plant communities. The caryopses (grains) of *Z.*

SIDA 17(3): 533–549. 1997

palustris (northern wild-rice) are an important food being harvested in the wild and from cultivated paddies in Minnesota, California, Ontario and Saskatchewan. *Zizania aquatica* (southern wild-rice), native to the Atlantic and Gulf Coastal Plains, is not cultivated, but has been grown experimentally. *Zizania texana*, a local endemic in southcentral Texas, treated by Terrell et al. (1978), was included in experimental studies by Duvall (1987) and Duvall and Biesboer (1988a, 1989). We further understand that technical studies are being carried on by Francis Horne (pers. comm.) in San Marcos, Texas.

Basal parts of the culms and rhizomes of the Asian species, *Zizania latifolia*, are edible when infected with the fungus *Ustilago esculenta* Hennings (Terrell & Batra 1982). It is important to note that the presence of the fungus prevents flowering. Living material of *Z. latifolia* should be banned from importation into North America because infection of our native species might have serious ecological and economic consequences.

Hitchcock (1951; revised by Chase) referred to *Zizaniopsis miliacea* (Michx.) Doell & Aschers. as "southern wild-rice," implying close relationship to *Zizania;* however, *Zizaniopsis* and its related genus, *Luziola* (including *Hydrochloa*), are quite distinct in important reproductive characters from *Zizania* and were later placed in a separate subtribe (Terrell & Robinson 1974; Duvall et al. 1993).

This paper provides keys, descriptions, distributions and synonymies for the North American species of wild-rice. Representative specimens cited are primarily those in the US herbarium. Recent publications concerning the taxonomy of *Zizania* are discussed, with emphasis on *Zizania palustris* var. *interior*.

SYSTEMATIC TREATMENT

Zizania L., Sp. Pl. 2: 991. 1753 [& Gen. Pl. ed. 5. 427. 1754]. *Hydropyrum* Link, Hortus Berol. 1: 252. 1827, *nom. illeg. Ceratochaete* Lunell, Amer. Midl. Naturalist 4:214. 1915, nom. illeg. by lectotypification. LECTOTYPE: *Zizania aquatica* L. [Reveal, Phytologia 72:6. 1992].

Melinum Link, Handbuch 1:96. 1829, nom. illeg. (non Medikus, Philos. Bot. 2:40. 1791). TYPE: *Melinum palustre* (L.) Link [=*Zizania palustris* L.].

Monoecious aquatic annuals or perennials. Culms stout or slender, erect or decumbent. Leaves with sheaths open, rounded dorsally; ligules membranous or scarious, glabrous; blades flat, linear to broadly lanceolate, apices acuminate to caudate. Panicles terminal, in American species the staminate spikelets on lower branches, pistillate on upper branches, in the Asian species *Z. latifolia* both types on same branches. Spikelets 1-flowered, disarticulating from the expanded cupulate apices of pedicels, glumes absent, lemmas as long as spikelets, paleas subequal to lemmas, narrower. Stami-

nate spikelets pendulous, caducous, lemmas and paleas membranous, loosely covering the 6 stamens, lemmas usually 5-veined, paleas usually 3-veined; anthers 3–10 mm long in our species, linear, yellow. Pistillate spikelets cylindrical, caducous, lemmas and paleas chartaceous or coriaceous, plicately clasped along their margins, lemmas 5-veined, terminally awned, paleas 3-veined, awnless; stigmas 1–2.5 mm long in our species, short-plumose, at anthesis laterally exserted. Caryopses cylindrical, hilums linear, embryos linear.

From *zizanion*, an old Greek name for a weed growing in grain.

KEY TO NORTH AMERICAN *ZIZANIA* SPECIES

1. Plants perennial; culms geniculate, stoloniferous, completely immersed or only upper parts of culms emergent; upper ligules acuminate or caudate; restricted to San Marcos River, Hays Co., Texas ..... 3. **Z. texana**
1. Plants annual; culms erect, not stoloniferous, rarely completely immersed; upper ligules often truncate or erose, occasionally acuminate; not along San Marcus River, Hays Co., Texas 2
   2. Fertile (bearing mature spikelets) pistillate inflorescences 10–50 cm wide, with widely spreading branches (immature inflorescences or those bearing only aborted spikelets may have appressed branches); lemmas of pistillate spikelets chartaceous (papery) and flexible, dull or sublustrous, bearing scattered short prickle hairs not or only slightly denser at lemma apices, lemmas and paleas sometimes partly separating along their margins at maturity; aborted pistillate spikelets 0.4–1 mm wide, often thread-like; plants to 4 or 5 m tall; leaf blades (3–)10–72 mm or more wide ..... 1. **Z. aquatica**
   2. Fertile pistillate inflorescences 1–10(–50 in var. *interior*) cm wide, with all or most of the branches upwardly appressed or in var. *interior* somewhat spreading ; lemmas of pistillate spikelets coriaceous (firm and leathery) or indurate (hardened), lustrous, sometimes whitish, glabrous or with hairs in lines, the hairs often densely grouped at lemma apices, lemmas and paleas tightly clasped along their margins; aborted pistillate spikelets 0.6–2.6 mm wide; plants 1–2(–3 in var. *interior*) m tall; leaf blades 3–20(–40 in var. *interior*) mm wide ..... 2. **Z. palustris**

1. Zizania aquatica L., Sp. Pl. 2:991. 1753.

Annuals with culms 0.2 to ca. 5 m tall, erect or decumbent, often stout, glabrous, most culms emergent or rarely immersed. Leaves with sheaths glabrous or scabridulous, margins ciliate or glabrous; ligules 5–30 mm long, upper ones ovate or triangular, truncate to acuminate, often erose or irregularly lobed; blades to 1.5 m or more long, (3–)10–55(–ca. 72) mm wide, scabrous or glabrate above and beneath, margins scabrous or glabrate. Panicles 20–120 cm long, (5–)10–50 cm wide; mature staminate branches ascending to widely spreading or reflexed, pedicel apices 0.2–0.6 mm wide; mature pistillate branches widely spreading or divaricate (sometimes appressed if immature or bearing only aborted spikelets), pedicel apices

0.5–1.2 mm wide. Staminate spikelets 5–12.5 mm long excluding awns, lemmas 1–2.5 mm wide, lanceolate, acuminate or with awns to 3 mm long, paleas with awns 0–2 mm long. Mature pistillate spikelets 5–24 mm long excluding awns, 1–2.5 mm wide, lemmas lanceolate or oblong, chartaceous, flexible, dull or somewhat lustrous, with numerous scattered short prickle hairs not or scarcely denser at lemma apices, mature lemmas and paleas often partly separating along margins, awns to ca 9 cm long, scabridulous; aborted pistillate spikelets 0.4–1 mm wide, linear, shriveled, often filiform. Caryopses 6–22 mm long, 0.8–2 mm wide. $2n=30$.

KEY TO THE VARIETIES OF *ZIZANIA AQUATICA*

1. Plants to 5 m tall; blades (5–)10–72 or more mm wide; pistillate spikelets 7–24 mm long; lemma awns to 90 mm long ..... 1a. var. **aquatica**
1. Plants 0.2–1 m tall; blades 3–12(–20) mm wide; pistillate spikelets 5–11 mm long; lemma awns 1–8 mm long ..... 1b. var. **brevis**

1a. Zizania aquatica L. var. **aquatica**. *Ceratochaete aquatica* (L.) Lunell, Amer. Midl. Naturalist 4:214. 1915. TYPE: without collector or data (LECTOTYPE: LINN 1119.1!; [Reveal, Phytologia 72:6. 1992]).

Zizania clavulosa Michx., Fl. Bor. Amer. 1:75. 1803. TYPE: North America: A. Michaux.
Hydropyrum esculentum Link, Hort. Berol. 1:252. 1827. *Stipa angulata* L. ex Steud., Nomencl. Bot. ed. 2. 2:642. 1841, as syn. of *Hydropyrum esculentum* Link. TYPE: North America.
Zizania aquatica var. *subbrevis* B. Boivin, Naturaliste Canad. 94:528. 1967. TYPE: CANADA. ONTARIO: Russell Co.: Casselman, 21 Aug 1884, *J.M. Macoun 28938* (HOLOTYPE: CAN).

Common name.—Southern wild-rice

Distribution.—In fresh or somewhat brackish marshes, swamps, rivers, streams, occasionally lakes. Coastal plain and locally in piedmont from New England and New Brunswick to Florida and west to southern Louisiana; from New England westward across southern Quebec and southern Ontario through the southern part of the Great Lakes region to central Ohio, northern Indiana and Illinois, southern 3/4 of Wisconsin, and rare in southern Minnesota; rare or absent in northeastern Iowa, western Kentucky and Missouri (Fig. 3). Occasionally introduced elsewhere for waterfowl food. A variant population in the Wading River area of southern New Jersey has narrow leaves and plants mostly immersed (Ferren & Good 1977; observed and collected in 1977 by Terrell and Ferren, and in 1983 by Duvall). Narrow-leaved populations occur locally in the New England states and near Ottawa, Ontario, and individual narrow-leaved plants occasionally occur elsewhere. Figs. 1, 3.

Selected representative specimens examined (US). CANADA. ONTARIO: Addington & Lennox Cos.: Napanee, along the Napanee River, 24 Jul 1952, *Dore 13840*. Carlton Co.: Marvelville, tributary of Castor River, 14 Sep 1973, *Dore & Carteret 21157*. Dundas Co.:

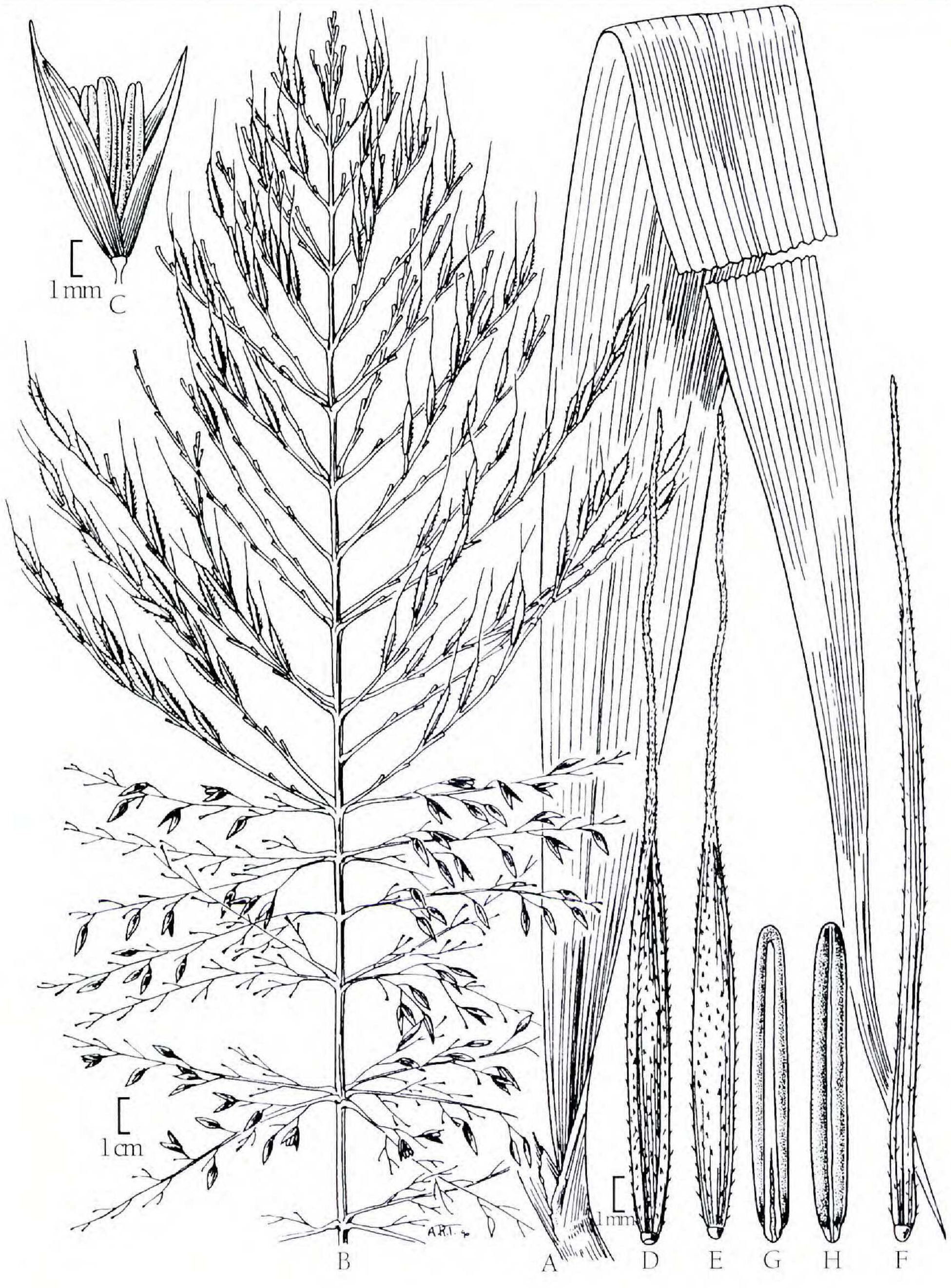

FIG. 1. *Zizania aquatica* var. *aquatica*. A. Culm leaf (*Terrell 4467*). Inflorescence (*Terrell 4911*). C. Staminate spikelet (*Terrell 4459*). D. Pistillate spikelet, ventral view (*Terrell 4467*, D-H). E. Pistillate spikelet, dorsal view. F. Aborted spikelet. G. Caryopsis showing embryo at base. H. Caryopsis showing hilum.

2 mi S of Marionville, Castor River, 14 Sep 1972, *Dore & Carteret 25159*. **Essex Co.:** Hillman, 19 Aug 1949, *Dore 10340*. **Frontenac Co.:** Verona, Hardwood Creek, 17 Aug 1951, *Dore & Mulligan 13549*. **Iberville Co.:** Henryville, South River, 12 Aug 1952, *Bassett & Hamel 2454*. **Leeds Co.:** 10 mi SW of Brockville, Jones Creek, 25 Sep 1950, *Dore 12895*. **Ontario Co.:** 3 mi E of Port Perry, Lake Scugog, 26 Aug 1949, *Dore, Senn, & Frankton 10310*. **Prescott Co.:** E of Alfred Station, Alfred Peat Bog, 12 Jul 1955, *Dore 16000*. QUEBEC: **Missisquoi Co.:** 2.5 mi N of Clarenceville, South River, 13 Aug 1952, *Bassett & Hamel 2505*.

UNITED STATES. ALABAMA. **Mobile Co.:** Mobile River, *Mohr s.n.* DELAWARE: **New Castle Co.:** Wilmington, 1 Sep 1897, *Commons s.n.* **Sussex Co.:** Nanticoke River at Woodland, 15 Sep 1976, *Terrell & Jones 4559*. FLORIDA: **Duval Co.:** Freshwater creeks, Oct, *Curtiss 3364*. **Marion Co.:** Dunnellen, Withlacoochee River, 9 Sep 1898, *Cambo 906*. **Orange Co.:** Cold Spring Creek, 23 Sep 1898, *Cambo & Baker 1139*. **Georgia: Bryan Co.:** Ogeechee River at bridge along Route 17, 7 Sep 1973, *Terrell 4467*. **Camden Co.:** White Oak Creek along Route 17, 8 Sep 1973, *Terrell 4470*. **Glynn Co.:** Altamaha River near Route 17, 8 Sep 1973, *Terrell 4469*. **McIntosh Co.:** Champney River along Route 17, 8 Sep 1973, *Terrell 4468*. KENTUCKY: Reelfoot Lake, 6 Oct 1915, *Alexander 308*. LOUISIANA: **Saint Tammany Par.:** vicinity of Covington, Sep 1919, *Arsene 11596*. **Maine: Barnstable Co.:** Harwich, Allen's Harbor Creek, 2 Sep 1918, *Fernald & Long 16183*. MARYLAND: **Anne Arundel Co.:** marsh along Patuxent River, 26 Aug 1973, *Terrell & Terrell 4460*. **Calvert Co.:** Chesapeake Beach, 18 Aug 1912, *Chase 6132b*. **Caroline Co.:** Denton, 6 Oct 1973, *Terrell & Terrell 4476*. **Dorchester Co.:** 1 mi NW of Sharptown, 15 Sep 1976, *Terrell & Jones 4565*. **Queen Anne's Co.:** Millington, 30 Sep 1973, *Terrell & Terrell 4475*. MASSACHUSETTS: **Middlesex Co.:** Cambridge, 26 Aug 1911, *Knowlton s.n.* MICHIGAN: **Berrien Co.:** New Buffalo, Margin of River, 20 Jul 1911, *Lansing 3279*. **Monroe Co.:** shores of Lake Erie, 27 Aug 1924, *Farwell 7077*. **Saint Clair Co.:** Port Huron, 12 Aug 1910, *Dodge 12*. NEW JERSEY: **Atlantic Co.:** 1-2 mi S of Green Bank along Route 563, 24 Sep 1977, *Terrell 4911*. **Burlington Co.:** Wading River just above Route 542, 21 Jul 1974, *Ferren & Good s.n.* NORTH CAROLINA: **Brunswick Co.:** 2 mi W of Wilmington, Brunswick River, 5 Sep 1973, *Terrell 4462*. **Chowan Co.:** Edenton, 20 Jul 1938, *Godfrey 5337*. **Jones Co.:** W of Pollocksville, Miry Hole Branch, 9 Sep 1966, *Bradley, Sears, & Bannister 3467*. PENNSYLVANIA: **Chester Co.:** West Chester, *Darlington s.n.* SOUTH CAROLINA: **Colleton Co.:** Combahee River at bridge on Route 17, 7 Sep 1973, *Terrell 4465*. **Jasper Co.:** 2 mi NE of Coosawhatchie, Tullipinny River, 7 Sep 1973, *Terrell 4466*. **Georgetown Co.:** Cat Island, 16 Aug 1915, *Alexander 100*. RHODE ISLAND: **Providence Co.:** Diamond Hill, 26 Sep 1942, *Palmer 46579*. VIRGINIA: **Charles City Co.:** Graves Landing, Chickahominy River, 10 Sep 1941, *Fernald & Long 13537*. **Fairfax Co.:** Hunting Creek, 20 Jul 1915, *McAtee 2377*. **Stafford Co.:** Potomac River at Aquia Creek, 28 Aug 1938, *Hermann 9744*. WASHINGTON D.C.: vicinis Washington D.C., 12 Sep 1880, *Ward s.n.* Roosevelt Island, 10 Oct 1958, *McClure s.n.* WISCONSIN: **Green Lake Co.:** Fox River, 2 mi W of Princeton, 23 Aug 1981, *Terrell 5016*. **LaCrosse Co.:** 4 mi E of LaCrosse, 22 Aug 1974, *Terrell 4487*.

1b. **Zizania aquatica** var. **brevis** Fassett, Rhodora 26:157. 1924. *Z. aquatica* subsp. *brevis* (Fassett) S. L. Chen, Proc. Int. Symp. Bot. Gard., Nanjing, China 600. 1990. TYPE: CANADA. QUEBEC: rocky tidal flats of St. Lawrence River, Levis, 9 Aug 1923, *H.K. Svenson & N.C. Fassett 853* (HOLOTYPE: GH; fragment US 2797822!; photo Dore 1969: 18).

Common name.—Estuarine wild-rice.

Distribution.—Occurs only in tidal mud flats along the upper St. Lawrence River in Quebec about 80 km upstream and downstream from Quebec City. Fig. 3.

Representative specimens examined (US). CANADA. QUEBEC. Tidal flats, Neuville, 23 Aug 1947, *Swallen 9703;* just west of Pierre Laport Bridge, Anse Grigras, 13 Aug 1983, *Darbyshire 2030*. **Levis Co.**: S of ferry dock along St. Lawrence, 13 Aug 1983, *Darbyshire 2031*. **Lotbiniere Co.**: Upper tidal flat of St. Lawrence estuary at Ste. Antoine des Fonds, 31 Aug 1947, *Dore 47-971*. **Portneuf Co.**: estuarine marsh of St. Lawrence, Portneuf, 9 Sep 1976, *Dore 25522*. **Quebec Co.**: upper tidal beach of estuary of St. Lawrence, Beauport Flats, 27 Aug 1975, *Dore 25471*.

2. **Zizania palustris** L., Mant. Pl. 2:295. 1771.

Annuals with culms to 2(–3 in var. *interior*) m tall, erect, glabrous, part or most of culms immersed. Leaf sheaths glabrous or with scattered hairs, margins glabrous; ligules 3–16 mm long, lanceolate to triangular, truncate or erose; blades 20–60 cm or more long, 3–20(–40 in var. *interior*) mm wide, glabrous, margins glabrate or scabrous. Panicles 24–60 cm long, to 20(–40 in var. *interior*) cm wide; mature staminate branches of panicle 3–20 cm long, branches ascending or spreading, pedicel apices 0.2–0.4 mm wide; mature pistillate branches of panicle 1–8(–15) (–50 in var. *interior*) cm long, appressed or ascending or 1–few branches spreading (to widely spreading in var. *interior*), pedicel apices 0.7–1.2 mm wide. Staminate spikelets 6–17 mm long excluding awns, lemmas 1–2.3 mm wide, lanceolate, acuminate or with awns to 2 mm long, paleas with awns 0–2 mm long. Mature pistillate spikelets 8–22(–33) mm long excluding awns, 1–2.6 mm wide, lemmas lanceolate or oblong, coriaceous or indurate, lustrous, sometimes whitish, glabrous or with short prickle hairs in lines, these hairs often more densely aggregated at lemma apices, mature lemmas and paleas remaining firmly clasped along their margins, awns to ca 9.3 cm long, hirsute at bases to scabrid distally; aborted pistillate spikelets 0.6–2.6 mm wide. Caryopses 6–30 mm long, 0.6–2 mm wide. $2n=30$. Fig. 2.

KEY TO THE VARIETIES OF *ZIZANIA PALUSTRIS*

1. Leaf blades 3—15(–20) mm wide; lower pistillate branches with 2–8 spikelets; pistillate inflorescences usually 1–10 cm wide, with appressed or ascending branches; plants to 2 m tall ..... 2a. var. **palustris**
1. Leaf blades (10–)20–40 or more mm wide; lower pistillate branches with 9–30 spikelets; pistillate inflorescences (5–)10–50 cm wide, with branches ascending to widely spreading; plants 1–3 or more m tall ..... 2b. var. **interior**

2a. **Zizania palustris** L. var. **palustris**. Mant. Pl. 2: 295. 1771. *Melinum palustre* (L.) Link, Handbuch 1:96. 1829. TYPE: garden plant grown at Uppsala (LECTOTYPE: LINN 1119.2!) [Reveal, Phytologia 72:7. 1992].

Z. aquatica var. *angustifolia* Hitchc., Rhodora 8:210. 1906. *Z. aquatica* subsp. *angustifolia*

FIG. 2. *Zizania palustris* var. *palustris*. A. Culm base (*Terrell 4496*). B. Inflorescence (*Terrell 4515*, B-G). C. Pistillate spikelet, ventral view. D. Pistillate spikelet, dorsal view. E. Aborted spikelet. F. Caryopsis showing hilum. G. Caryopsis, side view.

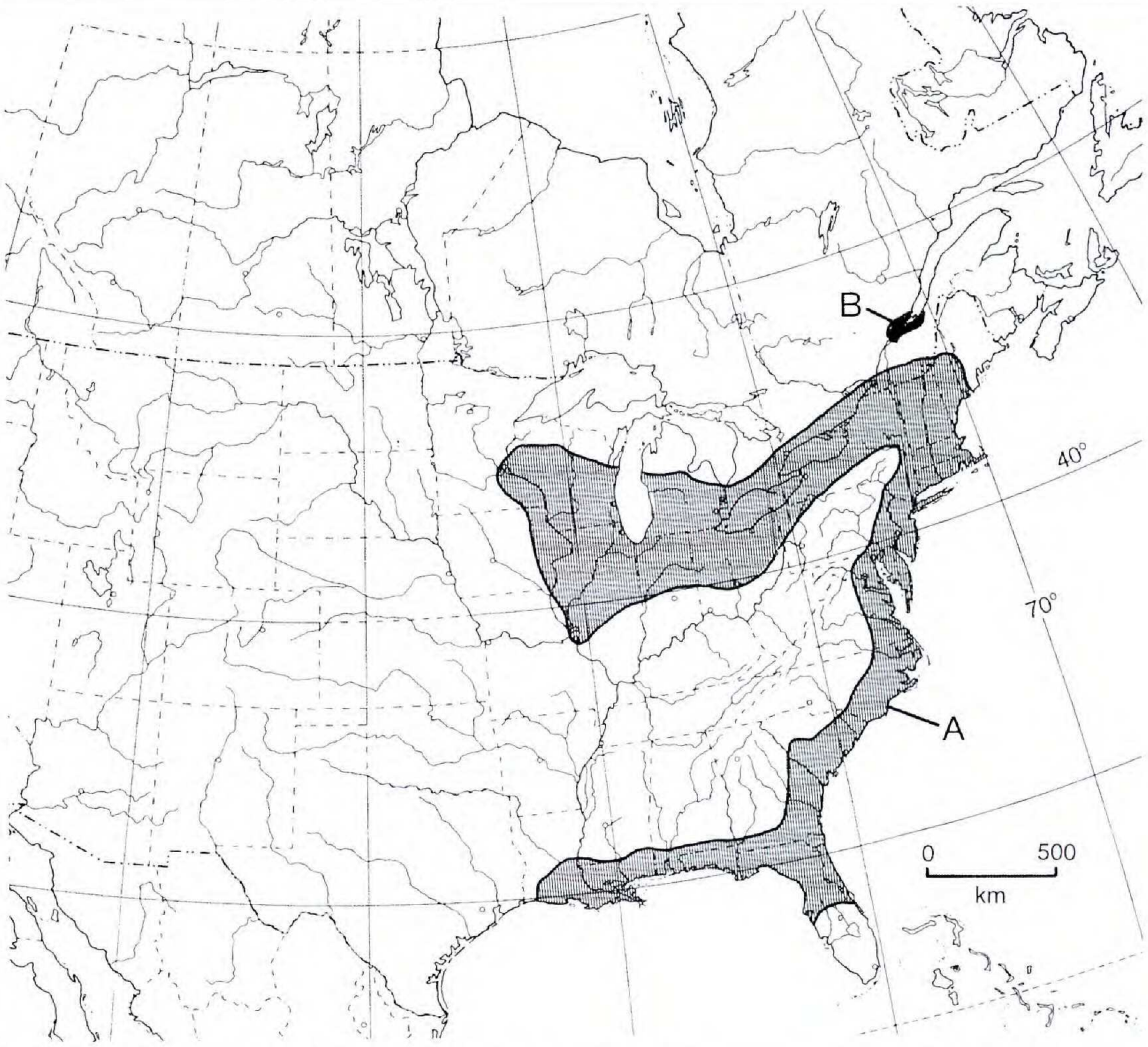

FIG. 3. Geographic distribution of *Zizania. aquatica* var. *aquatica* (A) and *Z. aquatica* var. *brevis* (B).

(Hitchc.) Tzvelev, Novosti Sist. Vyssh. Rast. 8:73. 1971. TYPE: U.S.A. MAINE: Belgrade, Aug 1895, *F. Lamson-Scribner* s.n. (HOLOTYPE: US 80339!)

Z. palustris forma *purpurea* Dore in McNeill & Dore, Naturaliste Canad. 103:565. 1976. TYPE: CANADA. ONTARIO: Russell Co.: in Castor River 2 mi E of Embrun, 21 Sep 1949, *W.G. Dore & R.J. Moore 10587* (HOLOTYPE: DAO).

Common name.—Northern wild-rice

Distribution.—In shallow water of lakes and streams, often forming extensive stands in northern lakes; Nova Scotia (introduced), New Brunswick, southern Quebec, and New England states westward across the Great Lakes states, central and southern Ontario, to central Alberta (range extended westward by planting fide Aiken et al. 1988), the Dakotas, and Nebraska. Occasionally planted elsewhere for waterfowl food, known to have been introduced but probably not surviving locally in British Columbia, Arizona, West Virginia, and Idaho. Fig. 4.

Selected representative specimens examined (US). CANADA. MANITOBA: near Winnipeg,

30 Jul 1933, *Chambliss 391*. NEW BRUNSWICK: **Westmoreland Co.**: Aulac, Chignecto Isthmus Marsh, 21 Aug 1945, *Dore & Ingalls 45-1068*. ONTARIO: Hemlock Island, Georgian Bay Islands, 25 Jul 1942, *McDonald 257*. Roundtable Lake, Hardwick Township, 20 Aug 1951, *Garton 1627*. **Addington, Co.**: 3 mi SW of Napanee, Napanee River, 16 Aug 1951, *Dore & Mulligan 13540*. **Carleton Co.**: Jock River, 11 Sep 1950, *Dore 12850*. **Frontenac Co.**: 8 mi SW of Arden, Salmon River, 14 Aug 1951, *Dore & Mulligan 13417*. **Leeds Co.**: 10 mi SW of Brockville, St. Lawrence River, 25 Sep 1950, *Dore 12898*. **Renfrew Co.**: Renfrew, Bonnechere River, 18 Aug 1952, *Cody & Parmelee 6598*. **Victoria Co.**: 2 mi E of Sebright, Head River, 20 Aug 1952, *Cody & Parmelee 6682*. QUEBEC: W of Lacolle, Lacolle Creek, 6 Aug 1952, *Dore & Cody 13918*. Noyan, Richelieu River, 6 Aug 1952, *Dore & Cody 13919*. **Chambly Co.**: Longueuil, 21 Sep 1924, *Victorin 18258*. **Labelle Co.**: Mont-Laurier, Petite River, 3–5 Aug 1941, *Marie-Victorin, Rolland-Germain & Blain 1*. **Nicolet Co.**: W of Becancour, St. Lawrence River, 11 Aug 1983, *Darbyshire 2017*.

UNITED STATES. INDIANA: **LaGrange Co.**: 2 mi E of Ontario, Pigeon River, 30 Aug 1914, *Deam 15045*. **Steuben Co.**: Lime Lake, 19 Aug 1916, *Deam 20913*. **White Co.**: 3 mi S of Buffalo, 24 Aug 1919, *Deam 29542*. ILLINOIS: Joliet, 22 Aug 1904, *Skeels 462*. IOWA: **Dickinson Co.**: Lower Gar Lake, 15 Aug 1957, *Thorne 18599*. **Fayette Co.**: 18 Jul 1894, *Fink 180*. MAINE: **Franklin Co.**: Farmington, Jul 1899, *Knowlton 314*. **Hancock Co.**: Long Island, Aug 1872, *Young s.n.* **Penobscot Co.**: Keg Stream, 28 Aug 1934, *Walker 2032*. **Sagadahoc Co.**: Bowdoinham, 14 Sep 1916, *Fernald & Long 12580*. **Washington Co.**: Princeton, 2 Sep 1932, *Chambliss 248*. MASSACHUSETTS: Concord, Sudbury River, 21 Aug 1904, *Worthen s.n.* MICHIGAN: **Allegan Co.**: Kalamazoo River above Allegan, 12 Sep 1902, *Wight 124*. **Emmet Co.**: Crooked river at Devil's Elbow, 9 Aug 1932, *Gates 17206*. **Huron Co.**: near Caseville, Saginaw Bay, 9 Sep 1910, *Dodge 14*. **Kalamazoo Co.**: SW of Vicksburg, Barton Lake, 21 Jul 1938, *Rapp 2178*. **Saint Clair Co.**: Lake Saint Clair, 12 Aug 1910, *Dodge 13*. MINNESOTA: **Cass Co.**: S of Deer River, Mississippi River, 31 Aug 1975, *Terrell 4507*. **Clearwater Co.**: Lake Itasca, 6 Aug 1929, *Grant 3016*. **Mille Lacs Co.**: near Mille Lacs Lake, 3 Sep 1975, *Terrell 4515*. **Otter Tail Co.**: East Battle Lake, Aug 1892, *Sheldon s.n.* NEBRASKA: Bone Creek, 29 Aug 1893, *Clements 2921*; near Halsey, 6 Aug 1934, *Martin 439;* Rat Lake, 14 Aug 1915, *Thomson 51*. NEW YORK: **Clinton Co.**: Plattsburg, Lake Champlain, 22 Aug 1917, *Hitchcock 16018*. **Jefferson Co.**: Woodville, along Lake Ontario, 23 Jun 1921, *House 8217*. **Oswego Co.**: Selkirk, Salmon River, 4 Aug, *Clausen & Hinkey 4289*. **St. Lawrence Co.**: Waddington, along the St. Lawrence, 22 Aug 1935, *House 20744*. NORTH DAKOTA: **Stutsman Co.**: Jamestown, James river, 22 Aug 1913, *Lunell s.n.* SOUTH DAKOTA: **Beadle Co.**: Huron, edge of James River, 23 Aug 1896, *Griffiths 118*. **Brookings Co.**: Brookings, Jul 1892, *Williams s.n.* VERMONT: West Haven, 18 Aug 1913, *Kirk 1042*. WISCONSIN: **Sawyer Co.**: Couderay Lake, 4 Aug 1930, *Williams 68*.

2b. Zizania palustris var. **interior** (Fassett) Dore, Publ. Dep. Agric. Canada 1393:20. 1969. *Z. aquatica* var. *interior* Fassett, Rhodora 26:158. 1924. *Z. interior* (Fassett) Rydb., Brittonia 1:82. 1931. *Z. palustris* subsp. *interior* (Fassett) S. L. Chen, Pro. Int. Symp. Bot. Gard., Nanjing, China 600. 1990. TYPE: U.S.A. IOWA: Emmet Co.: Armstrong, 27 Aug 1897, *L. H. Pammel & R. I. Cratty 764* (HOLOTYPE: GH; ISOTYPE: US 328087!; photo Dore 1969: 19).

Common name.—Interior wild-rice

Distribution.—Sporadically in eastern Canada and westward across the Great Lakes region to southern Manitoba and central Alberta (range extended westward by planting; see Aiken et al. 1988), Nebraska, Kansas (?),

Minnesota, Iowa, Wisconsin, Missouri, and southward (by planting?) in Illinois, Indiana, and Ohio). Fig. 4, 5.

Selected representative specimens examined (US). CANADA. MANITOBA: Starbuck, 20 mi W of Winnipeg, La Salle River, 16 Aug 1950, *Dore 12734*. ONTARIO: **Northumberland Co.**: 3 mi W of Hastings, Rice Lake, 3 Sep 1952, *Dore & Hammond 13981*. **Russell Co.**: 3 mi W of Cumberland, Ottawa River, 18 Aug 1953, *Jenkins & Dore 3532*. QUEBEC: **Chateaguay Co.**: Chateauguay River, Aug 1941, *Boivin 4425*.

UNITED STATES. **Illinois: Henderson Co.**: near Oquawka, 1871, *Patterson s.n.* **Madison Co.**: Margins of lake, 8 Sep 1891, *Eggert 286*. **Woodford Co.**: N of Spring Bay, 12 Sep 1938, *Chase 6181*. INDIANA: Fulton Co.: 1 mi SE of Grass Creek, Grass Creek, 9 Aug 1928, *Deam 46049*. IOWA: **Cook Co.**: Desplaines River, 10 Aug 1901, *Chase 1669*. **Hamilton Co.**: 3 mi S of Jewell, Little Wall Lake, 16 Aug 1936, *Hayden 10325*. **Linn Co.**: Cedar Rapids, 20 Jul 1895, *B. Shimek 68*. MINNESOTA: Fort Snelling, Minnesota River, 28 Aug 1891, *Mearns 776*. **Chippewa Co.**: Montevideo, Chippewa River, 28 Jul 1895, *Moyer 25*. **Itasca Co.**: SE end of Bass Lake, 2 mi NNW of Cohasset, 31 Aug 1975, *Terrell 4510*. **Pine Co.**: 3 mi W of Pine City, 24 Aug 1974, *Terrell 4491*. **Wabasha Co.**: river along rt. 84, N of Weaver, 25 Aug 1981, *Terrell 5020*. NEBRASKA: **Grant Co.**: 15 mi S of Whitman, 3 Aug 1893, *Tulen 1630*. WISCONSIN: **Buffalo Co.**: slough in backwaters of Mississippi River, 1/2 mi SSW of Nelson, 4 Sep 1975, *Terrell 4516*. **Trempealeau Co.**: delta of Trempealeau River, Perrot State Park, 24 Aug 1981, *Terrell 5017*.

3. **Zizania texana** Hitchc., J. Wash. Acad. Sci. 23:454. 1933. TYPE: U.S.A. TEXAS. Hays Co.: San Marcos River near San Marcos, Apr 1932, *W. A. Silveus 518* (HOLOTYPE: US-1537174!; ISOTYPES: K! US-1720531!).

Perennial with culms 1–2(–5) m long, decumbent, geniculate, rooting at lower nodes, stoloniferous, long-streaming in river currents or the upper parts of culms emergent. Leaf sheaths glabrous; ligules 4–12 mm long, caudate or acuminate; blades to ca 1 m long, to 13(–25) mm wide, glabrous. Panicles 16–31 cm long, 1–10 cm wide; mature staminate branches ascending or somewhat spreading, pedicel apices ca 0.3 mm wide; mature pistillate branches appressed or ascending, pedicel apices 0.5–0.9 mm wide. Staminate spikelets 6.5–11 mm long excluding awns, lemmas 1.2–2 mm wide, ovate or oblong, acute to acuminate, paleas usually awnless. Mature pistillate spikelets 9–12.5 mm long excluding awns, 1.2–1.8 mm wide, lemmas lanceolate, somewhat coriaceous, somewhat lustrous, with scattered short prickle hairs, apices scabrous or hispidulous, awns 9–35 mm long, with scattered hairs; aborted pistillate spikelets 0.7–1.5 mm wide. Caryopses grown in cultivation 4.3–7.6 mm long, 1–1.5 mm wide, 1/2–3/4 as long as their lemmas. $2n=30$. See Fig. 814 in Hitchcock (1951).

Common name.—Texas wild-rice

Distribution.—This species is restricted to a 2.4 km length of the headwaters along the San Marcos River, within the city limits of San Marcos, Hays Co., in southcentral Texas (Terrell et al. 1978). The neutral or slightly alkaline (pH 6.9–7.8) water temperature varies only 5° (20.4–25.5) C annually. Officially listed as an endangered species.

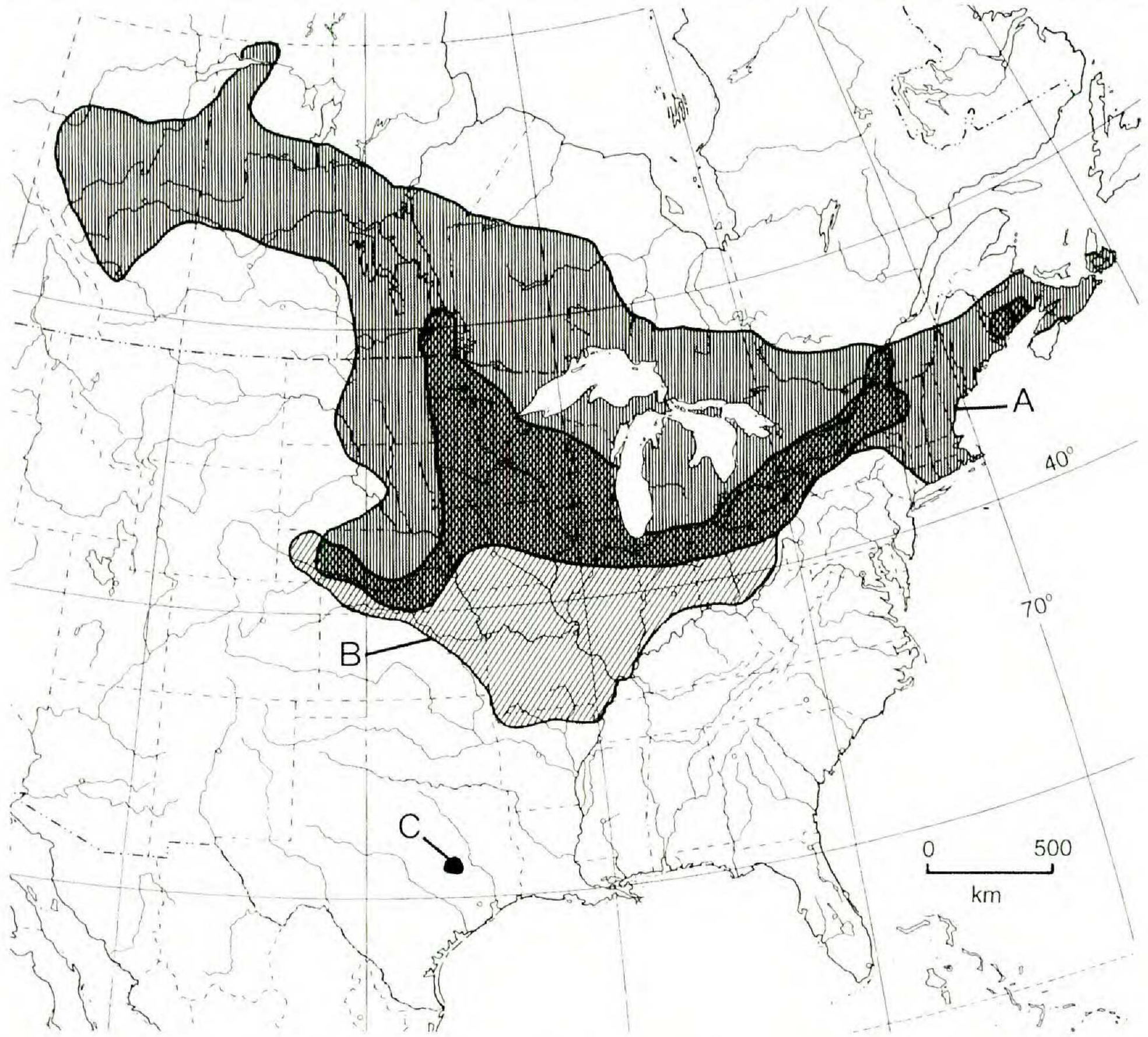

FIG. 4. Geographic distribution of *Zizania palustris* var. *palustris* (A), *Z. palustris* var. *interior* (B), and *Z. texana* (C). Central region shows overlap of A and B.

Representative specimens examined. UNITED STATES. TEXAS: **Hays Co.:** 1 mi below Spring Lake, San Marcos River, 14 Sep 1973, *Terrell, Emery & Beaty 4472* (US); San Marcos, Aug 1892, *Nealley 91* (MO, US); San Marcos, 6 Nov 1897, *Trelease s.n.* (BM, MO); "Marcos River," 31 May 1938, *Silveus 2731* (BM); San Marcos River, 14 Jan 1936, *Hotchkiss s.n.* (BM, MO).

EXCLUDED NAMES

Zizania effusa Munro, J. Linn. Soc., Bot. 6:52. 1862, nom. nud. Munro alluded to a specimen of *Phragmites australis* (Cav.) Trin. ex Steudel (LINN, 1119.3!), annotated by J. E. Smith with this name.

Other excluded *Zizania* names were listed by Fassett (1924).

DISCUSSION

In the past *Zizania palustris* (or *Z. aquatica* var. *angustifolia*) was generally included in *Z. aquatica* , the older name, in most publications (e.g.,

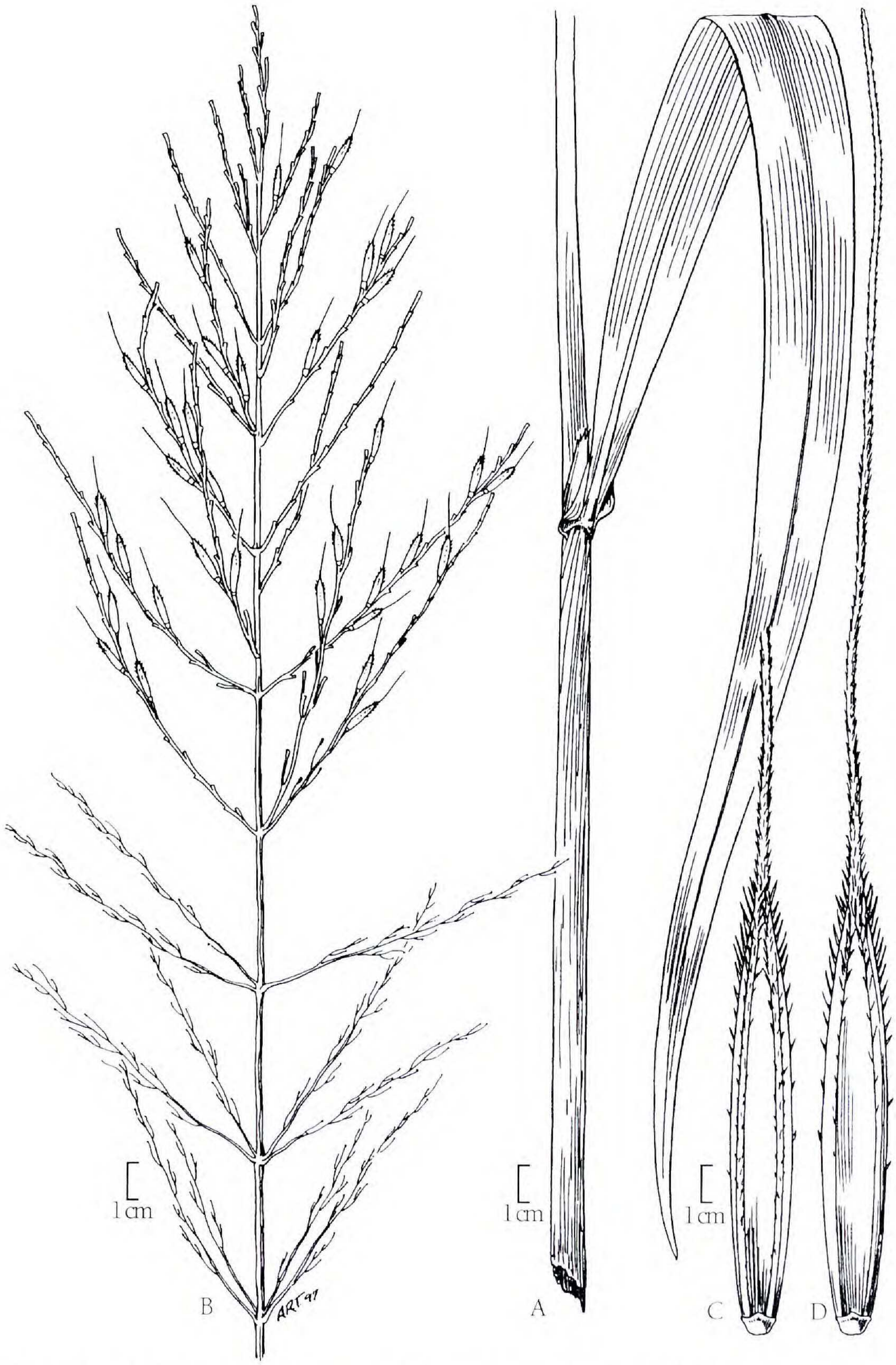

FIG. 5. *Zizania palustris* var. *interior*. A. Culm leaf (*Terrell 4516*, A-D). B. Inflorescence. C. Pistillate spikelet, ventral view. D. Pistillate spikelet, dorsal view.

Fassett 1924). However, Wiegand and Eames (1925) listed both Linnaean species in their flora of the Cayuga Basin. Dore (1969) recognized the two species in his monograph of the Canadian wild-rices. The two distinct species are borne out by morphological data: They differ in size of the plants, in leaf width, in size and branching of the inflorescence, and the lemmas and paleas differ in texture and thickness, with prickle hairs differing in their arrangement (see key to species). The caryopses differ slightly in length and thickness, but measurements overlap (see photographs of caryopses in Dore (1969), Dore & McNeill (1980), and Aiken et al. (1988)). The two species also differ in ligule size and shape, but these differences can overlap. Terrell and Wergin (1981) found differences in the shapes of the silica bodies in the lemmas: *Z. aquatica* usually has C-shaped silica bodies, whereas *Z. palustris* has suborbicular silica bodies with 1–3 shallow sinuses.

Present data on distribution show that the two species have distinct but overlapping ranges (Figs. 3, 4) with *Zizania palustris* the wild-rice especially of northern lakes and *Z. aquatica* centered in the southeastern Atlantic and Gulf Coastal Plains.

The marked differences in the spikelets of *Zizania aquatica* and *Z. palustris* were well-known to Fassett (1924) and undoubtedly to others (see the early literature cited by Aiken et al. 1988). Duvall and Biesboer (1988a), found an anatomical basis for the textural differences in the lemmas and paleas, there being a single layer of thin-walled subepidermal fibers in *Z. aquatica*, whereas *Z. palustris* (with its coriaceous texture) has at least two layers of thick-walled fibers.

Warwick and Aiken (1986), in an electrophoretic study, concluded that genetic identity values between *Zizania aquatica* and *Z. palustris* were on levels expected for congeneric species. They did not find any isozyme evidence for gene flow between the two species. However, Duvall and Biesboer (1988b), in a study of artificial hybridization, found that hybrids were produced (at a low level) only when *Z. aquatica* was the female parent. These authors concluded that (1) the "near-unilateral crossability barrier" supported the taxonomic distinctness of the two species, and (2) the successful artificial hybridization (although limited) shows the potential for successful natural hybridization.

Zizania aquatica var. *brevis*, native to a portion of the St. Lawrence River, has been studied in detail by Darbyshire and Aiken (1986). Warwick and Aiken (1986) found no isozyme differences with *Z. aquatica* var. *aquatica*. Similarly, Duvall and Biesboer (1989) found no distiguishing seed storage protein differences between var. *aquatica* and var. *brevis*. These two varieties were also found to be fully interfertile under greenhouse conditions (Duvall & Biesboer 1988b), supporting their recognition as varieties rather than as species.

In 1924, Fassett described Zizania *aquatica* var. *interior*, which resembles *Z. aquatica* in leaf width and inflorescence characters, but *Z. palustris* in the characters of the pistillate spikelets. Dore (1969) transferred var. *interior* to *Z. palustris*, and in this we follow Dore. Like *Z. palustris*, plants of var. *interior* have been purposely introduced to wildlife refuges and private wildlife preserves; consequently, it is sometimes difficult to determine whether a population of Interior wild-rice occurred naturally or introduced. Aiken et al. (1988) maintained var. *interior* as distinct, but noted that it is sometimes difficult to separate var. *palustris* from var. *interior*, and on their map of *Z. palustris* in Canada they did not attempt to separate them.

Zizania palustris var. *interior* occurs mainly where the ranges of *Zizania aquatica* and *Z. palustris* overlap (Figs. 3, 4); consequently it has been hypothesized that var. *interior* includes hybrids (Dore and McNeill 1980). Herbarium specimens of var. *interior* are mostly concentrated in the central United States. Field studies by the senior author in 1974, 1975, and 1981 in the Mississippi Valley of western Wisconsin and southeastern Minnesota produced several collections of var. *interior.* Fassett (1927) saw it "growing abundantly along the Mississippi River from Lake Pepin to Fountain City"; certain of these specimens exist at WIS. One of the Terrell collections (*4516* at US) included a range of morphological expressions varying from *aquatica*-like plants with broader leaves and more spreading pistillate branches to *palustris*-like plants with narrow leaves and compact appressed inflorescences (Fig. 5). These plants were like *Z. palustris* in spikelet morphology, thus agreeing with Fassett's (1924) original description of var. *interior*.

Cultivated strains of *Zizania palustris* have been selected by Minnesota growers for retention of mature spikelets to facilitate harvesting. In 1975, Terrell collected samples from several cultivars in Minnesota (vouchers at US). These were generally similar to *Z. palustris*, except in having some individuals bearing pistillate inflorescences with one or a few spreading or divergent branches, a condition called "crowfoot" by growers. Such plants are somewhat similar to *Z. aquatica*, which has spreading pistillate inflorescences. The electrophoretic study of Warwick and Aiken (1986) suggests that "Cultivated varieties, previously considered to be improved strains of *Z. palustris* var. *palustris*, were found to be more closely related to *Z. palustris* var. *interior* ... "

If var. *interior* is of hybrid origin we point out that the combination *Z.* × *interior* (Fassett) Rydberg (pro sp.) (Art. 50, Greuter et al. 1994; see also the present synonymy) is available for use. We also note that given not only the long expanse of evolutionary history but also the Pleistocene glaciations in particular it seems possible that var. *interior* could be the result of past introgressive hybridizations.

We emphasize, however, that some other evidence concerning var. *interior* argues against its origin as an interspecific hybrid. As noted above, Warwick and Aiken (1986) found no isozyme evidence of introgression between the annual species. A preliminary chloroplast DNA restriction sites study also failed to indicate that var. *interior* could be of hybrid origin (Duvall 1987). Even though an artificial hybridization study indicated that hybrids can be produced between the annual species, this study also showed virtually no difference in crossability between the two varieties of *Z. palustris* with those of *Z. aquatica* (Duvall & Biesboer 1988b). If var. *interior* were, in fact, of hybrid origin, one would expect it to (back) cross more readily with *Z. aquatica*, than does var. *palustris*. These data, coupled with the observation that all of the artificial F_1 hybrids that were produced in the hybridization study displayed the diagnostic spikelet characters of the *Z. aquatica* parent, is compelling evidence against the hypothesis of hybrid origin. These data suggested that vegetative similarities between *Z. palustris* var. *interior* and *Z. aquatica* var. *aquatica* are possibly an overlap of a morphological gradient of plastic and highly variable characters.

Unlike other North American *Zizania* species, *Zizania texana* behaved as a perennial in greenhouse experiments by Duvall (1987). A close relationship between *Z. aquatica* and *Z. texana* is supported by storage protein data (Duvall & Biesboer 1989) and distribution. However, crosses of *Z. texana* (ovulate parent) with three other taxa: *Z. aquatica* var. *aquatica*, *Z. palustris* var. *palustris*, and *Z. palustris* var. *interior*, resulted in hybrid progeny in only one case, that of *Z. texana* × *Z. palustris* var. *interior* (Duvall 1987). The pistillate spikelets of these hybrids were somewhat intermediate, unlike those of any other interspecific hybrid. Thus, full resolution of the relationships between annual and perennial species of North American wild-rice awaits further study.

ACKNOWLEDGMENTS

We wish to acknowledge the help of Mary Barkworth for advice on taxonomic descriptions. Alice Tangerini prepared the illustrations. Robert Soreng contributed helpful reviews of the manuscript. Work on this project is supported in part by Project F-12 of the Maryland Agricultural Experiment Station and Cooperative Extension Service.

REFERENCES

AIKEN, S.G. 1986. The distinct morphology and germination of the grains of two species of wild rice (*Zizania*, Poaceae). Canad. Field-Naturalist 100:237–240.

_____ P.F. LEE, D. PUNTER, and J.M. STEWART. 1988. Wild rice in Canada. Agriculture Canada Publ. 1830. New Canada Publ., Toronto. 130 pp.

DARBYSHIRE, S.J. and S.G. AIKEN. 1986. *Zizania aquatica* var. *brevis* (Poaceae): A 1983

distribution survey and a scanning electron microscope study of epidermal features. Naturaliste Can. (Rev. Ecol. Syst.) 113:355–360.

DORE, W.G. 1969. Wild rice. Canada Dept. Agric. Publ. 1393. Information Canada, Ottawa.

_____ and J. McNeill. 1980. Grasses of Ontario. Biosystematics Research Institute, Research Branch, Agriculture Canada Monograph 26.

DUVALL, M.R. 1987. A systematic evaluation of the genus *Zizania* (Poaceae). Dissertation, University of Minnesota, St. Paul.

_____ and D.D. BIESBOER. 1988a. Anatomical distinctions between the pistillate spikelets of the species of wild-rice (*Zizania*, Poaceae). Amer. J. Bot. 75:157–159.

_____ and D.D. BIESBOER. 1988b. Nonreciprocal hybridization failure in crosses between annual wild-rice species (*Zizania palustris* × *Z. aquatica*: Poaceae). Syst. Bot. 13:229–234.

_____ and D.D. BIESBOER. 1989. Comparisons of electrophoretic seed protein profiles among North American populations of *Zizania*. Biochem. Syst. Ecol. 17:39–43.

_____, P.M. PETERSON, E.E. TERRELL, and A.H. CHRISTENSEN. 1993. Phylogeny of North American oryzoid grasses as construed from maps of plastid DNA restriction sites. Amer. J. Bot. 80:83–88.

FASSETT, N.C. 1924. A study of the genus *Zizania*. Rhodora 26:153–160.

_____ 1927. Notes from University of Wisconsin–1. Rhodora 29:228–229.

FERREN, W.R., Jr. and R.E. GOOD. 1977. Habitat, morphology, and phenology of southern wild rice (*Zizania aquatica* L.) from the Wading River in New Jersey. Bull. Torrey Bot. Club 104:392–396.

GREUTER, W., F.R. BARRIE, H.M. BURDET, W.G. CHALONER, V. DEMOULIN, D.L. HAWKSWORTH, P.M. JORGENSEN, D.H. NICOLSON, P.C. SILVA, P. TREHANE, and J. MCNEILL (eds.). 1994. International code of botanical nomenclature. Regnum Veg. 131.

HITCHCOCK, A. S. (2nd ed., revised by A. Chase). 1951. Manual of the grasses of the United States. U.S. Dept. Agric. Misc. Publ. 200. Washington, D.C.

TERRELL, E.E. and H. ROBINSON. 1974. Luziolinae, a new subtribe of oryzoid grasses. Bull. Torrey Bot. Club 101:235–245.

_____, W.H.P. EMERY and H.E. BEATY. 1978. Observations on *Zizania texana* (Texas wildrice), an endangered species. Bull. Torrey Bot. Club 105:50–57.

_____ and W.P. WERGIN. 1981. Epidermal features and silica deposition in lemmas and awns of *Zizania* (Gramineae). Amer. J. Bot. 68:697–707.

_____ and L.R. BATRA. 1982. *Zizania latifolia* and *Ustilago esculenta*, a grass-fungus association. Econ. Bot. 36:274–285.

WARWICK, S.I. and S.G. AIKEN. 1986. Electrophoretic evidence for the recognition of two species in annual wild rice (*Zizania*, Poaceae). Syst. Bot. 11:464–473.

WIEGAND, K.M. and A.J. EAMES. 1925. The flora of the Cayuga Lake Basin, New York. Cornell Univ. Agric. Exp. Sta. Mem. 92.